

small shot, the chase was productive of nothing more substantial than excitement. From the experience gained from the race, the pace at which the seals go through the water may be considered between six and seven miles an hour.

Colonial Museum, Wellington.  
April 3, 1871.

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IV.—*On the Agamic Reproduction of a Species of Chironomus, and its Development from the Unfecundated Egg.*  
By OSCAR VON GRIMM \*.

[Plate III.]

*Introduction.*

“Nature goes on her way, and what seems to us an exception is according to rule.”—GOETHE.

ALTHOUGH the parthenogenesis, that is to say the agamic reproduction, of many insects (such as the worker bees, humble bees, wasps, ants, Coccidæ, &c.) had long been known, people were disinclined to put any faith in the discovery of Prof. N. Wagner, of Kasan, that the larva of a Cecidomyid propagates asexually. For fully two years Wagner's discovery had to submit to unmerited mistrust, although it had been crowned with the Demidow prize by the St. Petersburg Academy of Sciences; and it was only in the year 1863 that it was published in the ‘*Zeitschrift für wissenschaftliche Zoologie.*’ But however incredible the fact discovered by Wagner might appear, it had at last to be accepted when it was completely confirmed by the investigations of Meinert, Pagenstecher, Leuckart, Ganin, and Metschnikow. Nevertheless this alternation of generations among insects is regarded as an extremely rare case, although, in my opinion, we possess no satisfactory reasons for limiting it to a few insects; on the contrary, among the Diptera it appears to occur frequently, and although not in the greater number of these insects, still by no means only in a few isolated cases.

In the spring of last year (1869) I found in my aquarium a great number of ova, which afterwards proved to be those of a species of *Chironomus*, and which I employed for the investigation of the embryonic development. But when I surprised the egg-laying animal itself engaged in oviposition, I could not but subject it to a close examination, especially as it proved to be an imperfectly developed insect. I had conse-

\* Translated by W. S. Dallas, F.L.S., from the ‘*Mémoires de l'Acad. Imp. des Sciences de St. Pétersb.*’ 7<sup>e</sup> sér. tome xv.

quently to do with a case of asexual reproduction by an imperfectly developed insect; that is to say, I had before me an insect which is subject to what Von Baer calls *pædogenesis* \*.

But as I was obliged to interrupt my investigations during the whole summer, I resumed them in the autumn; and now, as it seems to me that I have attained to sufficiently interesting results, I venture to describe my researches, although I can perceive many deficiencies in my investigation.

### I. *Pædogenesis of the species of Chironomus observed.*

In the eggs detected by me there were developed larvæ 0·47 millimetre in length (Pl. III. fig. 2), and very similar in their structure to the larvæ of *Chironomus* described by Weismann †. They are transparent, clear, and of a yellowish colour, possess a large head, a broad thorax, and a nine-jointed abdomen, the segments of which are pretty sharply separated from each other. The mouth consists of two pairs of very strong brownish jaws (*md*, *mx*), of which the lower pair, having the median margins soldered together, is converted into an immovable lip. The small palpi (*p*) attached to the upper lip are chiefly serviceable to the larva in feeding. The antennæ (*a*) are large and composed of six joints, of which the last four form a style, which is surrounded at the base by six setæ; the basal joint bears a large seta, nearly equal in length to the second joint. On the sides of the head the little eyes (*e*) are situated, with some brownish points near them. The thorax possesses on its ventral surface a transverse fold, which is divided in the middle by a deep furrow, and transformed into a pair of clinging-feet (*ff*). These are furnished with claws, the number of which afterwards increases. As the development of the larva advances the feet become elongated, until finally, after the casting of the third skin, they reach to the mouth (fig. 3, *ff*). The last abdominal segment also possesses a pair of feet (*hf*), which are likewise furnished with claws, but much stronger ones than those on the anterior feet. Besides these we find at the same place four finger-like processes (*f*), which are seated close to the anus, and serve for the respiration of the larva ‡. The upper angle of this same segment is furnished with two tufts of very long hairs. In the interior

\* For K. E. von Baer on Prof. N. Wagner's discovery of larvæ that propagate, Ganin's similar and supplementary observations, and on pædogenesis in general, see Mém. Biol. de l'Acad. de St. Pétersb. tome v.

† Dr. A. Weismann, "Die Entwicklung der Dipteren im Ei, nach Beobachtungen an *Chironomus* sp.?, *Musca vomitoria* und *Pulex Canis*," Zeitschr. für wiss. Zool. xiii. p. 148.

‡ Weismann, *l. c.* p. 148.

of the larva the œsophagus, proventriculus (*pv*), stomach (*s*), and intestine are to be seen. The stomach is still filled with the remains of the vitellus. In the abdomen also we see the central nervous system, consisting of eleven ganglia: some of the anterior and posterior ganglia lie close together; but the middle ones distinctly show their double commissures.

This larva, constantly twisting about and working with its fore feet, whilst the hinder feet serve it rather as points of attachment, feeds upon the finest Algæ (*Spirogyra*), and at the same time surrounds itself with the detached filaments of the Algæ. These become interlaced by giving off side-shoots, and thus form a canaliform cocoon which is inhabited by the larva. Here it is constantly in motion, its abdomen twisting about in all directions; and this movement is indispensable to the larva, as by it the cocoon is widened and at the same time the deteriorated water contained in it is replaced by fresh. From time to time also the larva comes out and swims about very briskly in the water, still always moving in a serpentine manner. This occurs frequently at night. After such excursions the larva takes to the nearest cocoon without caring whether this belongs to itself or to another.

The larva grows very rapidly, so that within six or seven days it becomes four or five times its original length, and at the same time the second form of the metamorphosis, the pupa, is developed in it, the parts of which, such as the compound eyes, the feet, wings, &c., already shine very distinctly through the clear integuments of the larva (fig. 3). Even the ovaries do not slumber, ova are developed in them.

At last, after the third moult, the larva measures 4 millims. in length; its head has become much smaller in proportion; the fore feet have become elongated; the chitinous skin has acquired a very pretty, delicate rose-colour, which is most perceptible on the last abdominal segments, and is caused by the development of the pupa-skin\*. The movements of the larva in the cocoon become perceptibly weaker, and finally cease almost entirely. It then casts off the fourth skin, and thus becomes transformed into the very remarkable pupa.

The pupa (fig. 4) measures 3 millims. in length, and has a longish head, which, when seen from the side, is not unlike that of a cat, a thorax with three pairs of very long legs, and a nine-jointed abdomen, which is covered with an immense number of paired small hairs and longer single setæ. The

\* Leuckart, "Die Fortpflanzung und die Entwicklung der Pupiparen," Abhandl. der Naturf. Gesellsch. zu Halle, 1858, iv. p. 147.

sides of the abdominal segments exhibit longitudinal brown chitinous bands (*cb*), which serve as a support for the extremely delicate outer integument; these bands in the penultimate segment terminate in somewhat dilated lamellæ furnished at the margin with a few claw-like processes, which give them a still closer resemblance to a claw. In the middle of the lower surface of the same segment there are two oval apertures (*go*), through which the mature ova are expelled. Behind these is the smaller, but likewise oval, rudimentary anal orifice (*ao*). The very small terminal segment has on each side a rounded plate furnished on its margins with a series of very long and delicate hairs. At the boundary between every two abdominal segments a plumose hair is attached on each side to a cup-shaped cell; these are present also in the larva. The thorax is dilated on the dorsal surface into a shield (*pn*), which covers the head from above. At the sides of the thorax the embryonic wings (*w*) are attached, forming cases consisting of an extremely delicate membrane, which conceal within them the wings of the imago already formed and folded together. The wings of the perfect insect are developed even in the larva; for even in the youngest pupæ we may already see the hairs with which the wings are covered. The three pairs of legs are attached to the pectoral surface of the thorax; the first pair, seated at some distance from the posterior legs, have 4-jointed tarsi; the middle legs have 5-jointed, and the posterior again only 4-jointed tarsi. These legs are really the perfectly developed legs of the imago, only covered, in the same way as the wings, by a delicate envelope, through which the claws shimmer in the same way as the hairs of the wings. They are immovable; and being bent round the wings, they lie with these altogether upon the ventral surface of the pupa; so that all these structures together appear to the observer, at the first glance, exceedingly curious appendages; and this singularity of appearance is still further increased, because the pupa, in consequence of the wings lying thus upon its belly, swims about upon its back.

As already stated, the head of the pupa, when viewed from the side, is not unlike that of a cat. It is elongated and rounded off. At the sides of the head are the large, very prominent, pyriform eyes, between which the 6-jointed antennæ are attached. The mouth consists of a round aperture, which is situated at the apex of the conical cephalic appendage. The pupa has neither jaws nor proboscis, as it takes no nourishment. Superiorly this buccal appendage is covered by a row of strong and rather long setæ, the tips of which are approximate. The 4-jointed palpi are attached at the sides. Above



the head, on the pronotum, there are two thick filaments, which are described by Weismann, in the pupa of *Corethra plumicornis*, as stigmatic branchiæ (*sb*). Of stigmata our pupa, as living in water, is entirely destitute. The tracheal system is comparatively very small; it consists of a main tube running through each side of the whole body, which gives off a few small ramified branches, of which the thoracic branch is the most considerable. The central nervous system consists of eleven ganglia united to one another by double commissures. The greater part of the abdomen is now occupied by the ova, which are already perfectly developed and lie irregularly in the body-cavity. But when the pupa is dissected, it is still not difficult to detect the ovarian parts with the undeveloped ova.

This pupa, which has emerged from the larva in the cocoon, quits the place of its birth, and after swimming about for a short time, extrudes the ova contained in it through the above-described apertures situated in the penultimate ventral segment. These are now placed in a very regular row\* (Pl. III. fig. 1). They are, as has been stated, imbedded in a hyaline mass (*a*), and are attached by their whole surface to the glasses of the aquarium in the form of two cords, each 2.5 millims. in length. The pupa then dies; but in some cases, after depositing a small number of ova, it became further developed into the imago.

The case is quite different with the same pupæ in the autumn. Now, after undergoing the same development as in spring, differing in nothing except perhaps the much more considerable number of ova contained in them, they become transformed into the perfectly developed insect, a fly of the genus *Chironomus*, without depositing their ova. The abdomen of the escaped yellowish-green fly is shorter than that of the pupa, for which reason the two hindermost abdominal segments of the latter appear empty before the emergence of the fly. The pupa-case then bursts on the dorsal side; the fly first of all protrudes its abdomen, then draws the feet out of their tubes, then the head, and, lastly, the wings, which it finally unfolds, and then flies away, probably to deposit its fertilized ova, after copulation, again in the water.

\* It is worthy of remark that, if the ova are taken earlier out of the parent organism and placed in water, they always take the same position; that is to say, they place themselves in the same order in which we find them in the homogeneous mass after they have been deposited by the pupa. Even when they have been scattered too far apart, a small movement of the water suffices to cause them to arrange themselves in a row, as if they possessed some attractive power.

It is therefore an insect living principally in the water, perhaps living only for a day or two, or even a few hours, in another sphere.

But if we remove from the perfectly developed insect, before it has yet quitted the pupa-case, the ova which would otherwise have been subjected to fecundation, and preserve them in water, the development of the larva takes place in them also; it only lasts a little longer (about six days), and is frequently obstructed.

We have thus seen that our *Chironomus* is subject to an alternation of generations, namely to *pædogenesis*. But this case of *pædogenesis* is somewhat different from that of the *Cecidomyiæ*, in which the second generation is produced agamically by the larva, and not by the pupa. This, however, of course, is of no very great consequence. Von Baer has already expressed the opinion that different animals may be subject to *pædogenesis* at different stages of development\*. But, at any rate, our case of *pædogenesis* unites that of the *Cecidomyiæ* with the parthenogenesis of the Coccidæ, for example, especially because in the *Chironomus* the imago, which requires impregnation, is developed chiefly (perhaps, indeed, exclusively†) in the autumn—just as the Coccidæ produce their ephippial ova after copulation, and the agamic eggs without the cooperation of the male; but the larvæ of the *Cecidomyiæ* become converted into the imago, according to Wagner‡, when they find themselves under favourable conditions, without being subjected to the influence of the seasons. We shall see hereafter that both the structure and the development of the ova of *Chironomus* demonstrate this transition, inasmuch as they are perfectly identical with those of the Aphides and other insects, but not with those of the Cecidomyid larvæ.

Besides being subject to *pædogenesis*, our *Chironomus* appears to be not quite a stranger to parthenogenesis, at least in some instances, perhaps induced by artificial causes. Parthenogenesis, as is well known, is the designation of the agamic reproduction of perfectly developed but unfecundated females, to which worker bees§, humble bees, wasps, Psy-

\* "Ueber Prof. N. Wagner's Entdeckung &c.," Mém. Biol. de l'Acad. de St.-Pétersb. v. p. 280.

† The instances of the development of the imago in spring have perhaps been influenced by the temperature of the room and other artificial causes.

‡ "Beitrag zur Lehre von der Fortpflanzung der Insectenlarven," Zeitschr. für wiss. Zool. 1863, xiii. p. 524.

§ In the bees it occurs rarely; but among the wasps, humble bees, and ants it apparently occurs constantly (Leuckart).

chidæ, &c. are subject. The ova of the perfectly developed *Chironomus* are also developed, as we have seen, without fecundation, when they have been removed from the parent organism.

## II. The Development of the Ovary and Ova.

For the sake of clearness in discussing the developmental history of the ova, I must anticipate a little, and commence my description with the development of the ovary itself.

We shall see hereafter that the development of the embryo from the unfecundated ovum deposited by the pupa of our *Chironomus* is perfectly identical with that of the fecundated ova of the imago, which has also been found to be the case with the Cecidomyidæ\*. We shall see the development of the germ- or blastodermic cells; we shall see that, of the germ-cell formation, one germ-ball precedes another, inasmuch as it enters earlier into the blastema-layer, and here, surrounded by the protoplasm, becomes converted into the nucleus of a membraneless cell; this cell passes into the inferior polar space of the ovum, and divides here into two and then into four cells, which are indicated as polar cells (fig. 5). Leaving the discussion of the embryonal development for the present, I will now direct attention to these polar cells, as they are the primordial forms of the subsequent generation, the two next generations, the germinal vesicles of which combine, or, in one word, represent the germs of the ovaries and ova †.

With the advancing division of the germ-cells the bulk of the contents of the ovum increases, so that the polar spaces soon entirely disappear, and the polar cells, which were placed in the inferior, acute polar space, bury themselves in the layer of the formative vitellus or blastoderm. When we trace their destiny further, we find them (at the moment of the production of the primitive caudal furrow, which soon disappears, and is apparently of no importance in the further development of the embryo, but, according to Weismann, "must only be regarded as the earliest expression of the bilateral type in

\* Leuckart, "Die ungeschlechtliche Fortpflanzung der Cecidomyienlarven," Archiv für Naturg. 1865, p. 299.

† To these polar cells, which, according to Weismann (*l. c.* p. 208), are "so enigmatical," no embryologist, except Prof. Metschnikow, has paid any attention, or, at any rate, only Robin, who has founded upon them his theory of the origin of germ-cells by sprouting. Metschnikow was the first who recognized the polar cells in *Simulia* and *Cecidomyia* as the germs of the sexual glands. (See his 'Embryologische Studien an Insecten,' pp. 31-33 & 103-105; and Zhurn. M. H. Pr. 1865, Th. cxxvi. 5. p. 113.)

accordance with which the embryo is to be built up"\*) dividing into two groups (fig. 6), which then pass to the sides of the ovum. We then find that each of these groups, consisting of two nuclei, each with a nucleolar corpuscle, is surrounded by a homogeneous transparent mass, in which a few small hyaline corpuscles are enclosed. This mass has apparently been formed from the embryonal cells and the protoplasm of the polar cells, whilst the large nuclei with their nucleolar corpuscles, representing the nuclei of the polar cells, originate, as we shall see hereafter, from the germinal vesicles of the ovum or from the nucleus of the ovary of the preceding generation.

The nuclei of the embryonal ovary (fig. 7) increase by division; and the tertiary nuclei proceeding from them are each separately surrounded by a portion of the common protoplasm with the nucleiform embryonal cells contained in it; so that we may now regard the whole structure as a body which is composed of eight mutually independent cells: the protoplasm of these cells consists partly or, rather, chiefly of nuclei, *i. e.* embryonal cells. After the lapse of a certain time, when the embryo is already perfectly developed, the ovaries also have become more mature. We now find that the whole ovary has acquired a more elongated form; and from its superior extremity, or that directed towards the head of the embryo, there rises a thin filament, and the ovary itself encloses small corpuscles with a few nuclei, which represent the still imperfectly developed ovarian tubes.

In these embryonal ovaries, at the first glance, under a low power, we cannot overlook the agreement with those of the Cecidomyid larva as described by Leuckart†, Metschnikow‡, and Ganin§, and even with those of *Platygaster*, according to Ganin||. But, on a more careful examination of their further development, their difference becomes clear: they are in their whole nature perfectly similar to the ovaries of fully developed insects as described by Claus¶, Leydig\*\*, and others.

\* Weismann, "Die Entwicklung der Dipteren im Ei (*Chironomus*)," Zeitschr. für wiss. Zool. 1863, Bd. xiii. p. 115.

† "Die ungeschlechtliche Fortpflanzung der Cecidomyienlarven," Arch. für Naturg. 1865, p. 290.

‡ Embr. Studien an Insecten, Taf. 24. fig. 4.

§ Zapiski Imp. Ak. Pauk, 1865, vii. fig. 3.

|| "Beiträge zur Erkenntniss der Entwicklungsgeschichte bei den Insecten (*Platygaster*)," Zeitschr. für wiss. Zool. 1869, Taf. 30. fig. 3.

¶ "Beobachtungen über die Bildung des Insecteneies," Zeitschr. für wiss. Zool. 1864.

\*\* Der Eierstock und die Samentasche der Insecten, 1866.



In our larva they are concealed among the adipose bodies (*corpora adiposa*), being situated in the seventh abdominal segment on each side of the intestine (fig. 3, o), so that they can only be seen occasionally during the movements of the adipose bodies and intestine; and if we wish to study them more continuously, we are compelled to have recourse to compression with the glass cover, as has already been stated by Leuckart\*. Their intimate structure, however, can be studied only by preparation, by cutting or pressing them out.

To return to the developmental history of the ovary. The bodies, or composite cells, which we have seen in the embryonal ovary, representing the rudiments of the ovarian tubes, consist of a homogeneous protoplasm, in which the nuclei derived from the embryonal cells lie; among these nuclei the largest may easily be distinguished, as it only contains one nucleolar corpuscle, whilst the others, formerly embryonal cells, contain usually two, but sometimes even three. The large nucleus represents the nucleus of the cell, and originated, as we have already seen, from the nucleus of the polar cell; the whole structure, however, is nothing but a composite membraneless cell. Somewhat later we observe an elongation of this cell; and at the same time a membrane (*tunica propria*) is developed, which apparently originates from the protoplasm. Beneath this *tunica propria* there is a layer of fine epithelial cells, produced by the continued division of the embryonal cells.

The residuary nuclei of the ovarian tubes remain in the protoplasm, and now form the so-called *formative cells of the vitellus*; and the whole cell may now receive the name of an ovarian tube. Metschnikow, indeed, states that the formative cells of the vitellus originate from the nuclei of the polar cells, and the epithelial cells from the embryonal cells†, so that the ovum has nothing in common with the epithelial cells—"that the germ-cells stand in no genetic relation to the epithelial cells, and that only the germigenous and vitelligenous cells are of common origin"‡. But, in accordance with our direct observations, we must differ from Metschnikow's opinion, inasmuch as we deduce the genesis of both the vitelligenous and the epithelial cells from the embryonal cells.

These ovarian tubes, as we already know, pass into thin filaments, which are covered by a common membrane (the peritoneal envelope of the entire ovary), represent the undeveloped parts of the ovarian tubes§, and probably serve

\* *Loc. cit.* p. 290.

† *Embryologische Studien*, p. 32.

‡ *Ibid.* p. 104.

§ *Der Eierstock und die Samentasche der Insecten*, p. 49.

for the attachment of the ovary\*. But the question as to the course of this cord, and also as to its point of attachment, has remained unsolved by me. I cannot say whether it attaches itself to the Malpighian vessels, as in the Cecidomyid larvæ, according to Leuckart † and Metschnikow ‡, or to the adipose bodies on the one hand, and the intestine on the other, as is asserted of the same larvæ by Ganin §, or, finally, whether it runs to the dorsal vessel, as has been proved to be the case in many perfect insects by Leydig ||; for latterly I had very few young larvæ, and in older ones it is almost impossible to solve this question, as the ovary at this time becomes very tender, so that it breaks up into fragments at the least touch. Unfortunately I have never succeeded in making a preparation of a mature uninjured ovary—that is to say, at the time when some ova are already perfectly developed but have not yet fallen out into the body-cavity. Even when the ovary still appeared quite strong and uninjured, when it could still be pushed

\* It will be superfluous now to discuss the opinion of Johannes Müller that the lumen of this filament passes into that of the dorsal vessel, so that the whole of the ovarian tube would be nothing but an altered blood-vessel, and the ova be developed directly from the blood, seeing that, by Leydig's investigations, it is completely demonstrated that this union does not occur, and that only the peritoneal envelope passes into that of the dorsal vessel in some insects, whilst the ovarian tubes terminate cæcally before reaching the heart (Leydig, 'Der Eierstock &c.,' pp. 45-49). Moreover this was proved long before (in 1849, and therefore twenty years ago) by Meyer (Hermann Meyer, 'Ueber die Entwicklung des Fettkörpers, der Tracheen und der keimbereitenden Geschlechtstheilen bei den Lepidopteren,' Zeitschr. für wiss. Zool. Bd. i.), who expresses himself as follows:—"We often see definitely that this point *terminates cæcally* at the dorsal vessel; and by this alone the signification of a vessel (which has frequently been ascribed to it) would be contradicted, even if the recognition of the significance of this cord did not unconditionally exclude any such opinion" (*l. c.* p. 183).

† "Die ungeschl. Fortpfl. der Cecid.," Archiv für Naturg. 1865, p. 290, fig. 2.

‡ Embr. Studien, Taf. 24. fig. 4, and Zhur. Mni. Par. Pr. 1865, May, p. 107.

§ Zap. Imp. Ak. 1865, p. 46.

|| 'Der Eierstock &c.' It must, however, be remarked here that in the flies (e. g. *Musca domestica*) the ovaries do not attach themselves to the dorsal vessel (Leydig, *l. c.* p. 34). Meyer also, who has already been quoted, says, with regard to the Lepidoptera:—"A point (of the adipose body) regularly goes off anteriorly and attaches itself to the dorsal vessel; this subsequently serves for the attachment of the testis to the latter, and in the ovary it becomes the thread which runs from the anterior extremity of the ovary to the dorsal vessel" (*l. c.* p. 138). Under the name of the point (*Zipfel*) of the adipose body, Meyer means the peritoneal envelope of the ovary, as he himself states (p. 182), when he says the envelope "bears the character of an adipose-body lobe of the particular kind of adipose-body lobes which are arranged around the dorsal vessel."

to and fro with all its ova, the ova separated from one another and fell out of the ovary during its preparation, so that only rudiments of the ovary with a few undeveloped ova could be obtained. Notwithstanding this, I have thoroughly investigated the structure both of the entire ovary and of its individual parts. I frequently succeeded in extracting the ovary only partially, obtaining a fragment of the peritoneal envelope of the ovary, and a series of the remains of the ovarian tubes. These consist in the present case of not more than four chambers, reckoning even the least-developed one, representing the so-called vitelline or terminal chamber, according to Claus\*.

A perfectly developed ovary of our larva (fig. 8) consists of a bundle of ovarian tubes, of which we have counted as many as eight†; these ovarian tubes consist, as we have frequently observed‡, of an extremely elastic structureless membrane, lined internally with a layer of epithelial cells. The contents of these tubes consist of a ductile mass§, in which lie the vitelligenous cells, which usually contain several nucleolar corpuscles, and a larger nucleus with only one nucleolar corpuscle. By the division of these contents a whole series of compartments or germ-chambers are produced, in each of which is developed an ovum; so that such a many-chambered|| ovarian tube may be regarded as an egg-colony: comparing it, for example, to a Tapeworm—just as the latter consists of a series of independent individuals, which only cohere during the period of their incomplete development, and are arranged according to their degree of maturity, so also does the ovarian tube (but, of course, not its envelope) consist of a complete series of similarly arranged germ-chambers; those most highly

\* "Beob. über die Bildung des Insecteneies," Zeitschr. für wiss. Zool. 1864, p. 43.

† Their number is very different in different insects. Thus *Liparis auriflua* has four ovarian tubes (Meyer), and some Coccidæ as many as twenty (Leuckart, "Die Fortpflanzung der Rindenläuse," Arch. für Naturg. 1857).

‡ This is mentioned also by Claus (in *Lecanium*, l. c. p. 43), Leydig (l. c. p. 52), and others.

§ Meyer says it is albuminous (l. c. p. 191).

|| In each ovarian tube of many insects, as also in our *Chironomus*, several ova are constantly developed; but in others only one ovum is developed in each, as, for example, in *Lecanium* (Claus) and generally in most Coccidæ (Leuckart, "Die Fortpfl. der Rindenläuse," Arch. für Naturg. 1859, p. 216). However, no sharp limit exists between the single- and many-chambered ovarian tubes; for the ovarian tubes of some insects, as, for instance, *Chermes laricis* (Leuckart, l. c. p. 217), may be regarded as at once many- and single-chambered, because here the second germ-chamber is only formed after the complete development of the first.

developed are furthest from the terminal filament, and when they have attained a certain degree of maturity they fall apart like the proglottides of the Tapeworm.

The development of the ova, like that of cells, takes place by endogenous division. Each ovarian tube represents an elongated cell, as we have already seen; in this cell or tube the terminal portion of the contents with the half of the nucleus becomes constricted off (fig. 11), the nucleolar corpuscle having been previously divided\*. A cell thus cut off is the germ-chamber, which, after the deposition of the vitellus, becomes directly and completely converted into the ovum; and that portion of the ovarian tube from which the germ-chamber has been constricted off may be designated the vitelline chamber or terminal chamber†, so long as it has not yet given off the following germ-chamber. Then commences the constriction of the second or younger germ-chamber, and afterwards that of the third, and so on. The contents of the separated cells or germ-chambers, the future ova, consist of large round vitelligenous cells‡ (Stein). These vitelligenous cells extrude oil-drops, and at the same time become converted into the vitellus of the future ovum. The vitellus therefore originates from the same elements which have also formed the epithelial cells of the ovarian tube§. As the mass of the

\* From this it is clear that the nucleolar corpuscle by no means plays so unimportant a part as Leuckart, for instance, supposes (art. "Zengung," Wagner's Handwörterb. der Phys. Th. 4. p. 815); on the contrary, the nucleolar corpuscle appears, so to speak, to give the impulse of the division, superinduces the division of the nucleus, and therefore also the development of the germ-chamber corresponding to the ovum. But the nucleus appears to exert no such essential influence upon the division; for whilst it divides after the commencement of the constriction of the protoplasm, its function only commences subsequently. Lubbock says that the nucleolar corpuscle is only subsequently developed (see note *infra*, §).

† Claus, "Beobacht. über die Bildung des Insecteneies," Zeitschr. für wiss. Zool. Bd. xiv. p. 43.

‡ Meyer calls the vitelligenous cells *abortive ova*, and to their nuclei, as also that of the germinal vesicle, he gives the name of *germinal vesicles*; thus he says, "the germinal vesicles of the abortive ova (*i. e.* the vitelligenous cells) become filled with a colourless, more or less finely granular fat, and sooner or later lose their nuclei" (*l. c.* p. 192).

§ Lubbock (On the Ova and Pseudova of Insects) is of opinion that the vitelligenous cells and the germinal vesicles are only altered epithelial cells. His "vitelligenous cells" become converted into the ova in the following way:—The nucleus of a cell of the kind becomes converted into the germinal vesicle by the later development of the germinal spot (nucleolar corpuscle); the membrane of this cell disappears, and the vitellus collects upon it, having been secreted by other but similar vitelligenous cells; and finally the vitelline membrane is developed. He has found this to be the case also with the pseudova; but here he could not attain certainty as to the genesis of the germinal vesicle (Report by Dr.



vitellus increases, it collects in the lower extremity of the ovum; and the nucleus, which is already the germinal vesicle, descending from the upper extremity, buries itself in the constantly increasing vitelline mass. The chorion, however, is formed by the activity of the epithelial layer of the *tunica propria*; but whether this structure is formed as a cuticular deposit of the epithelial cells, as described by Leydig\*, or the epithelial cells are directly converted into the chorion, as stated by Stein†, I am unable to say‡.

It is therefore clear that the germinal vesicle of the ovum has originated from the nucleus, and the vitellus with the oil-drops and the chorion (corresponding to the epithelial cells of the *tunica propria*) from the vitelligenous cells, which represent the embryonal cells of the ovarian tube. But when we remember that the ovarian tube has been produced by the conversion of the polar cell, that the nucleus of the former (*i. e.* the ovarian tube) is only a portion of the nucleus of the latter (*i. e.* the polar cell), and the nucleus of the polar cell, again, is only a part of the germinal vesicle, we become convinced that this generation stands in direct connexion with the preceding one, and that its germinal vesicle is only a part of that of the first§.

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W. Kieferstein in 'Zeitschr. für rat. Medicin,' 1862, Bd. xiii. pp. 198, 199). The same opinion is also partially supported by Claus, who says that "epithelial cells, vitelligenous cells, and ova" (*i. e.* the germinal vesicles; but we have already seen that these are of different origin from the vitelligenous cells, and therefore we cannot agree with him) "are modifications of originally homogeneous elements, that they have proceeded genetically from the same cells, and by a different mode of development have attained such divergence of form" (*l. c.* p. 44). Stein thinks that the epithelial cells also take part in the formation of the vitellus; and Leydig is of opinion that they only secrete the chorion (Der Eierstock &c. p. 57); but nevertheless he admits their affinity to the ova in other animals, resting his opinion upon the investigation of La Vallette (*ibid.* p. 56, note 1). With regard to Metschnikow's opinion, *vide supra*.

\* Leydig very accurately describes the development of all the layers of the chorion in *Timarcha tenebricosa* (see his 'Eierstock und Samentasche,' pp. 11, 14, and 57, Taf. 2. figs. 7-10).

† Leydig, *l. c.* p. 59.

‡ Meyer ("Ueber die Entwicklung des Fettkörpers, &c.," Zeitschr. für wiss. Zool. Bd. i. p. 193) says that when the vitellus collects, the epithelial cells divide in the direction of the radii of the ovum, and lie with their outer ends on the chorion, and "strengthen it," and afterwards, "whilst the epithelial cells amalgamate with the chorion, they become thick-walled, unite firmly with each other, and lose their nuclei."

§ M. Ganin ("Beiträge zur Erkenntniss der Entwicklungsgeschichte der Insecten," Zeitschr. für wiss. Zool. 1869, p. 387) says:—"At any rate, it is clear that both the central cell and its nucleus (from which the embryo is developed) must be regarded as new formations." It seems to me, however, that this opinion is by no means correct, any more than Weismann's theory of the free formation of the germ-cells, which has recently been supported by Ganin in the Pteromalinae (*ibid.* p. 439).

#### 44 On the Agamic Reproduction of a Species of Chironomus.

This connexion will be rendered clearer by the following table:—

Ovum of generation 1.	=	Germinal vesicle.	+	Formative vitellus.	
Polar cell.	=	Nucleus of the polar cell.	+	Protoplasm.	Embryonal cells.
Ovarian tube	=	Nucleus of the ovarian tube.	+	Tunica propria.	+ Vitelligenous cells. + Epithelial cells.
Ovum of generation 2.	=	Germinal vesicle.	+		Vitellus. + Chorion.

The ovum, now fully developed, which originally, as we have seen, had an elongated form, contracts and acquires a spherical form. We see now that the vitelline mass, with the oil-drops enclosed in it, occupies one half of the ovum, the other half being still occupied by the vitelligenous cells; the nucleus of the germinal vesicle has disappeared; the epithelial cells have become fewer, for where the vitelligenous cells are placed, and where the vitellus is imbedded, they are no longer to be seen, being replaced by the chorion. The ovum does not long retain the spherical form; before it has become quite filled with the vitellus, its form again undergoes an alteration, becoming oval, and finally egg-shaped.

Both the summer (*pseudova*) and winter ova (*ova*) are developed in the manner above described\*. Moreover these two kinds of ova are not distinguished by their structure. Even resting only upon these two facts, we cannot, with Huxley, designate the one form as eggs (*ova*) and the other as false eggs (*pseudova*). It is true that fecundation is taken as the basis of this distinction, those ova which require fecundation for the development of the embryo being called *true*, and those which furnish the embryo without the aid of the male element *false* ova; but even if we are to rely upon the act of fecundation, we must distinguish the product of the development caused by fecundation from the product of the development which has taken place without fecundation, but not the ova, which truly, as Claus has stated quite correctly†, do not acquire the character of the product of the sexual organs by fecundation. Nay, the designation of the summer ova as

\* Lubbock has found the same thing: according to him the ova and pseudova are developed in accordance with one and the same type; but "he expresses himself more doubtfully with regard to the origin of the germinal vesicle in the pseudovum" (Keferstein).

† Claus, "Beobachtungen, &c.," Zeitschr. für wiss. Zool. Bd. xiv. p. 51.

false ova we regard as the less justifiable because, according to our observation already communicated, the development of the embryo also takes place in the winter ova without previous fecundation by the male.

Of course our opinion will lose nothing, even should it in time be proved that no evolution takes place without fecundation in the animal kingdom, *i. e.* that the cases of parthenogenesis and pædogenesis are only cases of self-fecundation.

It will not be superfluous to remark here, that in my judgment the fate of the parthenogenesis of plants awaits the theory of the agamic reproduction of some animals. As in the former case the parthenogenesis set up by Radlkofer and Alex. Braun has been brought down to the grade of ordinary hermaphroditism by the investigations of Regel, Karsten, De Bary, Schenk, and many others, so also it will probably be proved for the animal kingdom that some parts of the ovary produce spermatozoa instead of ova—which, indeed, may very easily be possible, as the ovary and the testis are originally perfectly similar structures.

Not long since I learned that H. Balbiani is now publishing his memoir upon the Aphides, in which he endeavours to demonstrate the hermaphroditism of those insects; and thus the supposition above expressed is already confirmed. Unfortunately I have been unable to make myself acquainted with this work.

[To be continued.]

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V.—*Contributions to the Fauna of the Upper Tertiaries.*  
No. I. *The "Mud-deposit" at Selsey, Sussex.* By ALFRED BELL.

IT is now some twenty years since Mr. Dixon, of Worthing, called the attention of geologists to a superficial deposit upon the sea-shore of the Sussex coast, near Selsey, eight miles south of Chichester, to which he gave the name of "mud-deposit." This deposit was afterwards fully described by Mr. Godwin-Austen in a paper upon the Newer Tertiary Deposits of the Sussex Coast, read before the Geological Society and published in their 'Quarterly Journal,' 1857. Both these gentlemen gave lists of fossils; but, owing to unfavourable circumstances, the beds or scattered patches being very inaccessible, and only workable at low tides, the lists only enumerate about forty-five species of various organisms. Some